

CHAPTER 11

Plant Defences against Animals in the Amazonian Rainforest

DANIEL H. JANZEN

Department of Biology, University of Pennsylvania, U.S.A.

CONTENTS

11.1. Introduction	207
11.2. The defences of Amazonian plants against herbivores: the rubber connection	208
11.3. Host specificity of Amazonian caterpillars	211
11.4. Patterns of chemical defences among plants and plant parts	213
11.5. Conclusion	216

11.1. INTRODUCTION

Plants stand still. This is as true in Amazonian rainforest as it is in boreal coniferous forest. As the architects of every medieval castle understood, if you are fixed in place, your past experiences (natural selection) lead you to develop (evolve) both intense standing defences and facultative ones. Furthermore, which defences are present at any given time reflect at least four quite different processes: how much resources you have to build and maintain, the traits of past and present attackers, and the structure of the entire edifice when a new defence is being considered. Finally, by the possession of ever more defences, the castle is rendered ever more immobile (physically, culturally), ever more a long-term investment, and ever more vulnerable if the defences are breached. Natural selection has generated the above pattern in plants just as it has done in humans, and in the lowland tropical rainforests of the world we find the epitome of the lesson. It is here that a plant stands against its herbivores with little or no help from cold winters, harsh droughts, irregular growing seasons, low species richness of herbivores or competitors, high quality population cueing systems, and all the other little ways (besides their intrinsic personal defences) that plants may use to defend themselves against animal herbivores or that may result in lower populations of herbivores.

However, I must at the outset emphasise that there is no single truly 'archetypical' lowland tropical rainforest. Many of the lowland tropical rainforests are covered by vegetation types which deviate in one

or more ways in the direction of extra-tropical systems. Amazonian rainforests are no exception: seasonal flooding of the Amazonian riparian forests, vegetation expansion and contraction during moisture cycles (see Absy and Prance, Chapters 4 and 8 this volume), occupation of soils so poor in nutrients that they are as hard on the tropical pyramid as is any northern winter (Janzen, 1974) (e.g. the drainage basin of the Río Negro), dry seasons well-defined in the calendar year and dry seasons of highly irregular depth and extent, etc. Such deviations provide the circumstances for the evolution of a variety of behavioural and strategic herbivore avoidance traits also characteristic of extra-tropical forests and tropical forests outside the lowland rainforests (e.g. seed predator and new leaf herbivore satiation at the population and habitat level; timing of leaf flushes with times of year that are difficult for herbivores; seed escape by submersion in water; escape from herbivores that have not yet reached the plant in geographic space or evolutionary time; escape from herbivores by growing where the physical conditions are too difficult for them).

The focus of this book is on Amazonian rainforest, a particular habitat with which I have no direct personal experience. However, the Amazonian rainforest has quite enough in common with lowland rainforests (or rather, with what is left of lowland rainforests) in other parts of the globe that one can write about it without ever having seen it. Such a great leap into the dark is made further reasonable by the fact that individual herbivores by and large display consistency in desires and behaviours the world over; the rumen environments of an arctic musk ox (*Ovibos*) and an Amazonian brocket deer (*Mazama*) have much more in common than do either their gross morphology or the habitats in which they live; an aristolochia swallowtail caterpillar (*Battus* spp.) in Texas, U.S.A. (Rausher, 1978), probably deals with the aristolochic acid in the *Aristolochia* leaves it eats in exactly the same manner as does an aristolochia swallowtail caterpillar in Manaus; and the seeds of *Hymenaea* pods in Amazonia are attacked by *Rhinochenus* weevils that are sister species to those which attack *Hymenaea* seeds throughout Central America (Lewinsohn, 1980; Janzen, 1974, 1975, 1978; Whitehead, 1976). Most of the astounding animal-plant interactions to be found in Amazonia are also to be found (or were to be found) in other sites in different combinations. One does not have to examine Brazilian *Cecropia* trees to evaluate the recent report (Andrade and Carauta, 1982) suggesting that because Amazonian *Cecropia* trees occupied by *Azteca* ants sustain conspicuous herbivore damage, the ants are not protecting the *Cecropia* trees; Wheeler (1942) made the same kind of deduction and observations on Central American ant-acacias and was as wrong (Janzen, 1966) for the same reason. In Amazonia, just as in Central America, the effectiveness of ants as protectors of plants cannot be determined without experimentally removing the ants and then observing what the herbivores do to the plants (see Janzen, 1973; Janzen and McKey, 1977 on the subject of *Cecropia*). I hope that the reader will forgive the tendency for the remainder of this essay to be a more generalised statement about defences against herbivores in tropical rainforests, rather than a focus on the essentials of Amazonian defences against herbivores.

11.2. THE DEFENCES OF AMAZONIAN PLANTS AGAINST HERBIVORES: THE RUBBER CONNECTION

Perhaps the Amazonian defence best known to the general public is rubber, the congealed latex of a tree (*Hevea brasiliensis*, in the Euphorbiaceae, the poinsettia and castor bean family). The latex, so cleverly removed by cutting the bark only deep enough to sever the laticifers (latex-containing ducts external to the cambium and phloem), serves the double defence function of all latices. When a boring insect (termite, scolytid, cerambycid, moth caterpillar, weevil larva) drills into the bark of a healthy living rubber tree (or chews into one of its leaves), it gets a 'face-full' and 'lung-full' of sticky congealing liquid, which is probably enough to stop almost any insect not specialised at dealing with



Fig. 11.1.a. Half-grown larva of *Lycorea cleobaea* resting on a portion of a leaf of *Carica papaya* that the larva has isolated by cutting a semicircular row of small holes through the leaf blade (arrow); following cutting the holes, latex flow is negligible from the isolated portion of the leaf as the caterpillar feeds.

Fig. 11.1.b. Same leaf as in a., but viewed from underside by transmitted light; row of small holes cut through the leaf (arrow) appears as small light dots. The remnants of other portions of isolated leaf segments are evident on both sides and the tip of the peninsular leaf projection.

latex (see below). Even if it can survive the mechanical effect of the latex there are also insecticidal chemicals in the latex. It is a striking commentary on the energy cost of this defence to the plant that once serious tapping of medium-sized rubber trees in a plantation begins, they increase in size at much slower rate and produce very few seeds, suggesting that their rubber production approaches the value of their net national product, so to speak. When the latex is not being removed at frequent regular intervals, the cost to the plant of maintaining this defence system is clearly much less but probably not trivial. Such an unchallenged standing defence is often thought of as a form of 'insurance' against herbivory, but the analogy is inappropriate. The cost of insurance purchases future recompensation for damages; the insurance does not deter the accident. A more appropriate and quite accurate analogy is the national defence budget. Just as in this budget, there are enormous costs not readily apparent in a cursory examination of the plant's phenotype. Furthermore, just as in national defence the real threat is extremely difficult to define and demonstrate unless the experiment of removing the defence system is conducted. In the same vein, the cost of maintaining the defence is generally much greater than the actual cost of the occasional losses when the defence system is penetrated; the true cost of herbivores clearly cannot be measured by just the amount of leaf they eat. Finally, just as in national defences, plant defences are rich in anachronisms and pleiotropisms.

Just as humans undoubtedly evolved the cultural trait of throwing a deadly projectile many times — the convergent evolution of biologists — latex is a defence trait that appears in many different quite unrelated families of tropical plants (Euphorbiaceae, Moraceae, Apocynaceae, Caricaceae, Asclepiadaceae, Guttiferae, Sapotaceae) and is itself very analogous to the convergent defence of resin and gum production in yet another set of tropical plant families. Not surprisingly then, a few herbivores have independently evolved quite similar ways to circumvent this defence (here is perhaps the place to remind the reader that all defences of plants have some species of herbivores that normally circumvent them). The striking black and white ringed caterpillar of the aposematic butterfly *Lycorea cleobaea* avoids the latex from the papaya (*Carica papaya*) leaves it eats by first cutting semicircular holes through them so as to isolate sections of the leaf blades (Fig. 11.1). The breaking of the laticifers causes the latex flow to the margin of the cut leaf to be halted and the caterpillar feeds without ingesting any latex. Since such a behavioural trait would work on any plant species whose defences include laticifers, it is not surprising

to find this butterfly's caterpillar also feeding on the leaves of figs (*Ficus* spp.) and milkweed vines (*Matelea trianaea*), and doing the same thing to these latex-rich leaves as it does to papaya leaves.

However, it is equally striking that *Lycorea* caterpillars do not feed on the latex-rich leaves of many other families and species of plants in the same rainforest habitats. The general statement is that each species of plant interacts with its potential herbivores through a characteristic set of defences that is in some way different from that of all other species of plants; secondary compound chemistry of each plant species is unique and distinctive in ways that matter to herbivores. The specific statement is that *Lycorea* may not be able to feed on other kinds of latex-rich leaves because (1) those leaves contain other secondary compounds besides those in latex and these compounds may be inimical to *Lycorea* caterpillars, and/or (2) the 'latex' of those leaves may be white and sticky like the latex of the leaves it eats but it is likely to contain quite different chemicals. It is at this point that thoroughness demands the addition of another factor which may be of equal importance but is both beyond the scope of this essay and is unfortunately traditionally left out of discussions of the defences of plants. *Lycorea* caterpillars may not be found on the leaves of the other latex-bearing species in the habitat because even if the butterfly puts its eggs there, the physical conditions and carnivore regimes (parasites and predators) of those species of plants eliminate the butterfly. Finally, we must not discount the possibility that the 'failure' of *Lycorea* to use these other plants as hosts may be a simple anachronism (e.g. Janzen and Martin, 1982). That is, they may be quite suitable hosts but the butterfly has not yet, if it ever will, come up with the appropriate mutations leading it to respond to those plants with oviposition.

In the usual ecologist's tradition, we have now discussed briefly the defence traits and latex properties of the rubber tree, and herbivore responses to them. But the rubber tree is good for more than that. It also allows us to examine the relationship of defences to resource availability and habitat-wide patterns in defences. It is no accident that rubber was a highly successful plantation crop growing on some of the worst tropical soils in the world — the sandy podzols of peninsular Malaya, generated by eons of leaching of granite with no periodic inundations of the sea. These soils are so poor that generally they were not farmed by shifting or fixed-field cultivators prior to rubber planting, nor is the pressure at present to turn them to this use. Further evidence is in the form of the consideration that the caloric value of the rubber generated by a sustained yield rubber plantation is pitifully small compared to, say, that of rice production on nearby alluvial bottomlands; rubber is a crop not because of its food value (its biological content or yield, so to speak) but because of its strategic value outside of the ecosystem. So why do rubber trees survive on poor soils? Because one of their native habitats is white-sand soils or similar podzols in the Amazon; it is a specialist at running its motors on low intake of low quality fuel. And the possession of a copious latex defence along with the numerous other nasty chemical defences characteristic of the Euphorbiaceae is not accidentally encountered in a tree that is a specialist on very poor soils. Rubber is a specific example of the general case that the worse the resource base for a plant, the better protected one expects the plants that grow there to be. In the tropics, without winter on the plant's side, this by and large means more protective chemistry.

The rationale is quite straightforward in theory (Janzen, 1974), and matches observations of places such as the vegetation of the Río Negro drainage moderately well. The harder it is for a plant to replace lost tissues (and their contained mineral ions) taken by an herbivore, the more intense should selection be for those traits that prevent herbivory. This might be termed the 'rich man spendthrift' hypothesis. And the worse the soil (or other resource base), the harder it is to replace a loss due to herbivory (note that losses due to defence budgets may be subject to the same kinds of selection, but the outcome may well be more recyclable defences and more clever defences rather than fewer of them). The outcome should be an increasing intensity of herbivore defences along a gradient of increasing soil sterility. I should be quite clear at this point that there is a severe herbivore threat in *all* Amazonian forest types, and that chemically well-defended plants likewise occur in *all* Amazonian forest types; it is the matter of degree that is under discussion.

But white-sand soils have more growing on them than just latex-rich (and resin-rich) plants. They are notorious the world over for producing blackwater rivers such as the Río Negro. These rivers derive their name from the large amounts of dark-coloured polyphenols (or tannins, the source of the colour of tea) in their water (and the absence of particulate erosive materials of latosol origin that would obscure the dark colour imparted by the tannin colloids). The tannins have only one origin — the foliage of the woody plants growing over the soil drained by blackwater rivers. But tannins are prominent among the foliage defences (as well as wood and bark defences) of many species of trees, including those growing on latosols and other kinds of lowland tropical soils more rich in nutrients than are white-sand podzols. Why do they end up in the streams in bulk when the vegetation grows on white-sand soils? There are clearly at least two answers. First, the vegetation itself appears to be richer in tannins on such sites than on latosols. Second, it appears that the soil-litter-microbe complex does not degrade tannins and tannin-rich foliage as fast on white-sands as on more fertile soils. This is likely due to (1) a lower nutrient content of the falling foliage (the worse the site, the more is extracted from a leaf before it falls), (2) a lower (slower) rain of partly processed material in the form of caterpillar dung (the worse the site, the lower the biomass of herbivores that it sustains), (3) a lower litter fall rate (the worse the site, the more intense the selection for evergreen leaves with more than a year lifespan), (4) a higher tannin content of the foliage that does fall, and (5) a lowered ability of soil microbes (including fungi) to degrade tannin-rich foliage residue as the availability of other nutrients declines.

And what do the tannins in leaves do to the herbivores that eat them? In the water of a blackwater river they chelate everything from themselves to calcium ions to the proteins on the oxygen-exchange surfaces of insect and fish gills. In the tanner's vat they bind with collagen to render the protein in a hide unavailable to bacterial enzymes — they 'tan' leather. The simple answer used to be that in the herbivore's gut they tanned the proteins of the gut wall, the bacteria in the gut lumen and the proteins released from the leaf by the herbivore's chewing (rendering them unavailable to the herbivore or its microbes). It is now becoming clear that the many different kinds of tannins respond differently to these three ecological groupings of substrate; at certain insect gut pH values, for example, a tannin may be quite inactive. To complicate the story even further, it is now clear that tannins are treated just like other defences by certain kinds of herbivores in that they may be actually used by the herbivore in its own metabolism (e.g. Bernays and Woodhead, 1982) and thereby become a nutrient from the herbivore's viewpoint.

11.3. HOST SPECIFICITY OF AMAZONIAN CATERpillARS

As an educated guess, any square kilometre of Amazonian rainforest containing members of the populations of about 500 species of plants will be fed on by at least 2000 species of caterpillars of Lepidoptera (moths and butterflies). Two core questions leap to mind. How are these species spread over the various plant parts? That is to say, what fraction of the caterpillars are young leaf-eaters, old leaf-eaters, seed-eaters, stem-borers, etc. Second, how are these species spread over the various plant species? That is to say, do most of the species of caterpillars have only one species of host plant, many species, or some complex pattern of these two alternatives? Inherent in the latter question is the idea that it is the defences of the plants (and primarily their chemical defences) that produces the pattern observed through interactions with the ability of the insects to get around these defences. It is the latter question that I wish to address below, though the processes involved apply also to answers to the first-posed question.

First, even a small amount of collecting and rearing caterpillars will make it quite evident that there is no such thing as 'the caterpillar' or an 'average caterpillar' when it comes to host specificity. Different taxonomic groups display quite different patterns. It is a safe bet that in the Amazonian rainforest

certain families of Lepidoptera will be quite different in their host specificity. For example, it is an easy prediction that for each of the 40–80 species of sphinx moth caterpillars (Sphingidae) there is only one or at most 3–4 (rarely) species of host plants. If there is more than one host for a species of caterpillar, the hosts will be closely related. Almost all of these host plants will belong to families that are famous for having members whose foliage is rich in toxic small molecules and/or latex, and none of the host plants will be in the Leguminosae. By way of striking contrast, for each of the 30–40 species of silk moth caterpillars (Saturniidae) there will usually be from 2 to many species of host plants, one species of caterpillar will feed on quite unrelated species of plants, many of the host plants will be species related to species notorious for high tannin content in foliage, and many of the host plants will be in the Leguminosae and Malvales (assuming that these families occur in the study plot). Additionally, there will be very little overlap in the list of sphingid hosts with the list of saturniid hosts (Janzen and Waterman 1984). Furthermore, it will be found that for a sphingid and saturniid larva of the same final body weight (weight just before pupation), the sphingid larva attains that weight in a significantly shorter period than does the saturniid.

Such a set of observations on the large caterpillars of two such widespread moth families leads to a characterisation of each that clearly relates to the impact that the chemical defences of their host plants have had on the moths' evolution. It appears that sphingid caterpillars are extreme specialists at, among other things, possessing the appropriate enzymes for degrading or otherwise avoiding the suite of specific small and quite toxic molecules to be found in a particular plant. They are therefore able to maximally use the nutrients in the relatively defenceless host plant, but able to feed only on the particular host plant for which they carry the appropriate enzymes. Since closely related plants are more likely to have similar defence fingerprints than are distantly related plants, if they have more than one host plant they are likely to be closely related. Such a way of doing things places a strong emphasis on the adult moth's ability to locate a host plant of the appropriate species and one with leaves at the appropriate stage of development so as to contain a defence profile which best complements the caterpillar's enzymatic abilities. Saturniid caterpillars appear to be extreme specialists at, among other things, possessing the appropriate gut milieu and growth rates to exist on a diet rich in tannins; the tannins would both lower the digestive efficiency of the gut process and render much of the protein in the leaf unavailable to the caterpillar. Here the answer appears to be able to grow slowly, process a lot of food, and get comparatively little out of each mouthful. Since tannins apparently show much less diversity in their chemistry than do such things as the alkaloids, cyanogenic glycosides, cardiac glycosides, etc. being dealt with by the sphingid larvae, and since the caterpillar is basically tolerating the tannin's effects rather than detoxifying it, such a caterpillar might be expected to be able to feed on many species of plants. The more the plant relies on a purely polyphenol defence system, the more it would appear to be susceptible to a saturniid caterpillar. Here, the ovipositing moth should have much more latitude in her choice of host plants, and the evolution of her choices should be determined in great part not so much by what kinds of polyphenol defences the plant has, as how much nutrient material is left over after the digestion-inhibiting processes have taken their toll. It will not now come as a surprise to the reader to find that sphinx moth adults are long-lived and feed at flowers through their adult life, developing a few eggs at a time. Saturniid adults do not feed as adults, live only a few days, and lay their entire clutch of several hundred eggs in 2–5 nights. As the caterpillars can feed on numerous species of plants, the females can be less specific in their choice of oviposition sites (and therefore can find them faster). Likewise, plants may be evolutionarily chosen through their abundance and nutrient content as much as through their defensive chemical traits (see Janzen 1984 for an elaboration).

In our hypothetical square kilometre of Amazonia there are more than sphingids and saturniids. A close look at the other families of caterpillars will reveal probably 1000 species of Noctuidae, Pyralidae and Notodontidae combined, acting largely like sphingids, and Lasiocampidae, Megalopygidae, Arctiidae, and Limacodidae acting largely like Saturniidae. Butterfly caterpillars (Nymphalidae,

Papilionidae, Pieridae, etc.) will act largely like sphingids in their host specificity.

Discussed above is the response of the animals that map their resource harvest onto a diverse array of plant defences. For each species of caterpillar there are one to a few species of plants where the chemical defences either make no difference or if responded to, it is often by using the very chemicals that deter all other herbivores as metabolic building blocks and signals to locate the plant. In a crude sense, the caterpillar may even evolutionarily view the defensive chemicals as important in keeping potential competitors from feeding on its host plant. At the other extreme, the caterpillar may view virtually all other species of plants that it encounters as simply unacceptable as food either because of direct perception of the secondary compounds as repellent or because the plant lacks the chemical fingerprint that tells the caterpillar to 'eat here'.

11.4. PATTERNS OF CHEMICAL DEFENCES AMONG PLANTS AND PLANT PARTS

The herbivores adjust their feeding in the vegetation according to their abilities, both evolved as part of that adjustment and ecological as part of the response to a new habitat that occurs when the herbivore first arrives. However, the pattern of defensive chemicals that any given herbivore or herbivore array interacts with is a combination of things evolved during the actual interaction and traits that are the result of other herbivore–plant evolutionary interactions. When a tapir (*Tapirus* spp.) picks and chooses among the many species of forest floor saplings to browse (Janzen, 1982), many of the chemicals that deter him were in fact probably evolved in response to selection by herbivorous insects, or if by browsing mammals, most of those that were responsible disappeared during the Pleistocene extinctions. The agouti sniffs and rejects a newly fallen soft legume seed; the lectins, alkaloids, protease inhibitors, cyanogenic glycosides and/or uncommon amino acids that render the seed inedible to this rodent constitute a defence repertoire whose traits have been selected by millennia of repelling parrots, climbing rats, bruchid beetles, monkeys, weevils, squirrels, agoutis, ground sloths, pyralid moth larvae, spiny rats, termites, fungi, bacteria, etc. The canavaine used by a bruchid as a major nutrient in a *Diolea* seed (Rosenthal *et al.*, 1978) may well have been evolved in response to all or part of the other kinds of seed predators, and the bruchid simply adjusted its physiology to the changing defences as the centuries passed.

With the varied fluctuating selective pressures by herbivores on the one hand, and all the internal design and cost constraints on this or that defence on the other hand, it seems little short of a miracle that any pattern in chemical or secondary chemical defences would occur. However, such patterns do occur and I suspect that many more will appear as we map out the potential defence repertoires of tropical plants (a major stumbling block is the habit of searching for one class of compounds across many plant taxa, rather than taking the plants in a habitat and working out the distribution of all defensive compounds in those plants — largely because the work has been done as mining for organic chemicals, not as a search for biological understanding).

By some surveys, twice as many tropical plant species contain alkaloids as do extra-tropical ones (Levin, 1976). With the exception of certain resins and terpenes from conifers and a few odd sources of tannins for the tanning trade, tropical plants have been vastly more important in generating a variety of pharmacologically active compounds than have extra-tropical sources, and this resource is just beginning to be tapped. But what of our hypothetical square kilometre of species-rich Amazonian rainforest? If you want an edible seed (one low in defensive chemicals), pick something with the hardest indehiscent nut wall around it, one that is dispersed regularly by rodents that also survive on it, or one that is wind-dispersed with synchronous fruiting at greater than yearly intervals (it helps if the seeds are smaller than normal). Trees that produce very large crops of small seeds are much more likely to have seeds edible to humans than are trees with a small crop of large seeds (especially if they fruit annually). The other side of

that coin is that if you are searching for seeds rich in exotic alkaloids, uncommon amino acids, lectins, etc., pick the largest soft seed you can find on the forest floor (if it was dispersed by being regurgitated by a large bird, so much the better). Likewise, if the tree occurs in nearly monospecific patches and fruits annually, its seeds are likely to be especially lethal.

Turning to the vegetative parts of plants, a best guess for food for a cow or tapir is a fast-growing deciduous sun-loving tree of riverbanks and other natural disturbed areas. An ant-plant without its ants is a sure bet for edibility to an enormous array of herbivores. At the other end, a truly evergreen tree with long-lived leaves growing in heavy shade is nearly guaranteed to generate stomachaches and worse for the 'generalist' herbivore. The same applies to the evergreen in full sun on white-sand soils. However, there are many ways that the particular capabilities of the vertebrate herbivore can render these generalisations ineffective in specific cases. A captive Costa Rican tapir accepted the foliage of virtually all species of early secondary succession vegetation except for *Trema micrantha* (Ulmaceae) a plant that by all reasoning should be highly edible; the same animal rejected the foliage of 42 species of woody legumes (ate one, *Pterocarpus rohrii*, in bulk) but ate about half of the species of legume vines that it was offered (Janzen, 1982).

Insects, with their gut specialisations to a small fraction of the total set of species in the habitat require a quite different perspective of chemical patterns. In the sphingid example mentioned above, caterpillars were commonly found on members of the Rubiaceae, yet Rubiaceae are well known for alkaloid-rich plant parts the world over; however, one of the rubiaceous food plants of two sphingid species, *Calyophyllum candidissimum* is also fed on by at least three species of saturniid caterpillars. Preliminary screening (P. Waterman, pers. comm.) shows this plant to have no alkaloids in the foliage and a moderate level of tannins.

The distribution of defensive compounds within the plant makes life difficult for the ecologist attempting to understand what physiological abilities are involved in various levels of host specificity. Growing tissues (cambium, ovules, apical meristems) characteristically have their chemical defences poorly developed and if an insect such as a sucking bug (Pentatomidae, Lygaeidae, Pyrrhocoridae) feeds on this plant part on a number of plant species, it may well not be at all versatile in its gut chemistry. On the other hand, a caterpillar that feeds on just one species of plant may well have to deal with several dozen quite different chemical defences as it consumes the blades and petioles of branches in the sun and shade, of old and young leaves, of leaves that have been fed on earlier in the season (and thereby carry induced defences as well as their standing defences). It is quite striking to watch a saturniid moth caterpillar eat all the old (mature) leaves from a branch and studiously avoid the new and expanding leaves (and shoot tip) at the branch end.

The tree trunk offers an especially visible example of heterogeneity of defences (Fig. 11.2). Starting at the outside, the bark is dead tissue thoroughly laced with secondary compounds in their most active, nonglycosylated forms (to avoid self-intoxication, many defence compounds in living tissues are stored attached to a sugar molecule, which renders them inactive until the appropriate enzyme in the animal or released by the broken cell splits off the sugar — e.g. cyanogenic glucosides, cardiac glycosides, alkaloid glycosides). Furthermore, it has virtually no nutrients in it to compensate for the damage potentially caused by its ingestion. Virtually no herbivores consume dead bark on the standing tree (except for some termites). Just below the bark lies an area of expanding and nutrient-rich tissues (bark cambium, phloem, cambium) which may be rich in defences but in a finely structured manner; the laticifers and resin ducts are missing from the cambial layers, the phloem may be rich in alkaloids that are quite missing from the cambium, etc. The defences are particularly active in this area, depending on a living and healthy tree. When a tree is stressed and the oleoresin or laticifer pressure falls (and the phloem flow to the active tissues ceases), this portion of the trunk is quickly invaded by a variety of boring beetles that were previously kept out by the active defences; they find a thin shell of very nutrient-rich tissues that they compete for with many other organisms. Moving into the xylem (sap wood), except for the



Fig. 11.2. Axe cut into trunk of 1 m diameter *Enterolobium cyclocarpum* (Leguminosae). The secondary compound-rich dead heartwood is bordered by the pale sapwood, which in turn has large drips of exuded gum from the gum vessels of the inner bark and phloem area. The bark and water-soluble gum are the outer defences of the living trunk, the heartwood the inner defences (Guanacaste Province, Costa Rica).

storage parenchyma (largely free of defensive compounds) we enter an area whose primary defence is its high water content, its largely indigestible (to an animal) cellulose structure, and its sandwiched position between the active defences of the bark-phloem area and the heartwood (see below). Once the outer defences are breached during tree death, the sapwood becomes the home and food of a great biomass and variety of animals that carry cellulose-degrading symbionts in their digestive systems or inoculate them as fungi. It is a striking characteristic of all of these animals that there can be no coevolution between them and their host plant, since the host plant is already dead or consigned to death when they enter (this does not apply to those much smaller number of species that may actually be the cause of tree weakening by massive attack, e.g. Scolytidae and sometimes Cerambycidae).

Finally, we reach the best protected portion of the tree, the heartwood — so prominent as the highly valued centre of a log that finds its way into beautiful furniture and veneers. This portion of the tree has died and as part of the senescence process, the cells were generally filled with tannins, terpenes, lactones, alkaloids, and a wide variety of other compounds in their most active unbound and unglycosylated state. When a rainforest tree falls, it is common for the sapwood and materials external to that to be degraded within a few months or a year, while the heartwood persists as a high quality log, degrading only very slowly as leaching by rainwater gradually removes the secondary compounds and allows fungi and termites to invade. Ironically, the tree sometimes appears to lay down less protective material in the centre of the heartwood, perhaps as a trait adaptive in that it results in the tree having a hollow ('rotted') core. This site becomes a haven for numerous animals which defecate and urinate in the cavity, thereby creating a small pocket of heavily fertilised soil that in fact may be mined by the tree responsible for it (Janzen, 1976). In other words, we have the herbivores to thank for the finest of the tropical hardwoods and those blemishes that bother the forester may be adaptive to the tree.

We have the herbivores to thank for more than latex, resin and tropical heartwoods (i.e. hardwoods of commerce, by and large). Fruits are perhaps the most complex of all the plant parts in the tropical rainforest, at least with respect to their chemistry. The biological function of a fruit is to get the seeds into the right place and keep them out of the wrong place. Since the entire herbivore array is a potential

threat to immature fruits, and since nearly all the herbivores are a potential threat to ripe fruits (except for the very select few that actually disperse the seeds to a place that raises the fitness of the tree), it is the chemistry of that defence that is responsible for many of the different flavours (and other traits) that we enjoy (or dislike) in fruits. Of course, fruits have differentiated with respect to the (sometimes coevolved?) likes and dislikes of the proper dispersers as well. The striking absence of a bountiful harvest of commercial wild fruits from Amazonian rainforest (in contrast with the mangos, mangosteens, rambutans, lichees, durians, jackfruits, etc. of southeast Asian rainforests) is not coincidentally related to the fact that the Amazonian rainforest lacks a fauna of large primates with flavour preferences that could be expected to be similar to those of humans.

11.5. CONCLUSION

It may seem that I have not said much about Amazonian rainforest or even about tropical forests, since it is quite clear that much of what I have said applies to vegetation the world over. This is true, it does. What is unique about the Amazonian rainforest is not at the level of principles as I have dwelt on; it is at the level of the maximum variation on the many themes that I have briefly outlined. When a serious fruit chemist goes to work on a commercial fruit, 50–500 kinds of secondary compounds come to light (flavours, repellents, fungicides, antibiotics, odours, ripeners, hormones, colours, seed germination inhibitors, digestible structural agents, in addition to the varied vitamins, minerals, proteins, fats and carbohydrates put in the fruit as bait for this or that dispersal agent). Multiply that by the 2000–3000 species of plants whose seeds interact with animals in any Amazonian rainforest of several square kilometres in extent. Furthermore, it is a safe bet that each of those plants carries another 50-plus kinds of herbivore defence compounds in its leaves.

Plants are not the only organisms with multipliers like those above. It is a fair guess that there are more species of leaf-eating caterpillars in 10 km² of Amazonian rainforest on its better soils than occur in the eastern half of the United States. The possibility for fine-tuned interactions among these animals and their plants in one direction, and their carnivores in the other direction are simply beyond our wildest imagination.

However, to round out this all too brief essay, I should close by noting that there are some truly dramatic surprises in store, of which we have only an inkling. For example, there is evidence accumulating that despite the incredible increases in herbivore species richness that occur in moving from extra-tropical latitudes to lowland tropical rainforests, the carnivores that feed on them do not increase proportionately, at least with respect to the insects. It may turn out that the highest species richness of hymenopterous parasitoids per unit area are in mid-latitudes, rather than in the tropics (Janzen, 1981); a potential cause is easy to spot — the more species-rich the hosts, the fewer there are per average population, and the tougher life is for either a generalist or a specialist parasitoid. An Amazonian rainforest may then turn out to be the place where we can expect to witness just how herbivore populations are controlled when parasitoids become a relatively minor form of mortality.

The moths mentioned earlier offer another example of surprises. I work in a lowland tropical deciduous forest in Costa Rica, far ecologically and geographically from the Amazonian rainforest. Yet a very large number of the species of moths at my study site have distributions that include the lowland rainforests of Brazil; they also range up into Mexico. Yet the plants their caterpillars eat in Costa Rican deciduous forests are almost without doubt different species and genera from those they feed on in the Amazon; again, it is through the comparison of the Amazonian populations with the Costa Rican populations that we may come to understand what kinds of circumstances generate adults so similar that the taxonomists call them the same species, yet have larvae that differentiate among different host plants.

The ecology, physiology and biochemistry of plant defences impacts on far more than some lonely caterpillar looking for lunch. The caffeine, tannin and myriad of as yet chemically undefinable chemicals that give a Brazilian cup of coffee its value on the London market are there because of what African rainforest animals did to *Coffea arabica* seeds and fruits for millions of years.

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